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BIOLOGICAL BULLETIN

INTER-PERIODIC CORRELATION IN THE ANALYSIS OF GROWTH.

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I. Introductory.

In the literature of growth, mathematical equations to describe changes in the actual size of the organism, or changes in the growth rate, are finding continuously widening applications. One has merely to refer to the papers by Robertson, Miyake, Moeser, Ostwald, Reed and Holland (1919), and Reed (1920)¹ for illustrations.

The criticism usually directed against such work is that in the higher organism, growth is a highly complex process, and that in consequence it cannot be represented mathematically. It is because of the very fact that growth is a complex process that mathematical analysis of the experimental data is necessary. Corollary to this must be the recognition of the fact that since growth is not a simple process, no one mathematical formula will be adequate for full description² and no one method adequate for complete analysis.

Our purpose in the present note is to illustrate on a series of data collected by one of us (1919) the application of inter-periodic correlation coefficients to certain phases of the problem of growth.

Before passing to the analysis, which is the special purpose of this paper, definition of the terms which will be used and a note

¹ Citations of literature may be traced from Reed's paper.

² Those who consider the possible adequacy of a single equation take the ground that if it be possible to represent the growth of an organism by a simple equation, it may be by virtue of the fact that during growth the various (often conflicting external) factors which affect the living substance are integrated by the organism.

on the nature of the data on which the statistical methods are illustrated are in order.

By growth stage we mean any given moment of time at which a series of organisms are measured. It is, therefore, synonymous with age during the growth period. The absolute size of the organism or of one or more of its parts at a given growth stage is the only character of the organism available for consideration.

By growth period we understand the period of time elapsing between the sth and the s + nth growth stage.

The increase in size during any such period we shall designate as a growth increment.

By relative growth increment, i_{rs} , we understand the ratio of the growth increment, i, to the absolute size of the individual at stage, r, where r and s are any two successive stages.

Turning now to the question of the original data as given in Table I. of Reed's (1919) publication we note from a study of the physical constants for absolute size in Tables I. and II. that there is an increase in the mean height of the plants up to the 77th day.

TABLE I.

STATISTICAL CONSTANTS FOR SIZE AT VARIOUS GROWTH STAGES.

Growth Stage.	Mean.	Standard Deviation.	Coefficient of Variation
7	17.931	1.617	9.0
14	36.328	4.786	13.2
21	67.845	8.932	13.2
28	97.672	14.673	15.0
35	130.724	19.174	14.7
42	168.707	24.801	14.7
49	205.397	32.760	16.0
56	229.672	37.842	16.5
63	247.345	42.574	17.2
70	251.776	43.433	17.3
77	253.810	43.767	17.2

The increase from the 63d to the 70th and from the 70th to the 77th day is relatively slight, being only 4.43 cm. or 1.79 per cent. of the height for the 63d day in the first case and only 2.03 cm. or 0.81 per cent. of the value for the 70th day in the second case. The difference between the 84th day and the 77th day is negligible. In view of the fact that there is no appreciable growth in

the sense in which the term is used here between the 77th and the 84th day, this period will be left entirely out of account in the calculation of the correlations for the following discussions.

Furthermore by considering the constants for growth increments as shown in Table II., we note that the coefficients of varia-

TABLE II.

STATISTICAL CONSTANTS FOR GROWTH INCREMENTS FOR VARIOUS GROWTH PERIODS.

Growth Period.	Mean Increment.	Standard Deviation.	Coefficient of Variation
7 to 14	18.397	3.764	20.5
14 to 21	31.517	5.164	16.4
21 to 28	29.827	7.907	26.5
28 to 35	33.052	7.505	22.7
35 to 42	37.983	11.578	30.5
42 to 49	36.690	14.266	38.9
49 to 56	24.276	16.540	68.1
56 to 63	17.672	13.803	78.1
63 to 70	4.431	4.713	106.4
70 to 77	2.034	5.096	250.5

tion for growth increments from the 63d to the 77th day are abnormally great. This may be in part due to biological causes, but it is doubtless due to a considerable extent to the relatively large error of measurement when the increment is very small in comparison with the size of the organism. If this be true, we should expect the correlations for actual size for the 63d to the 84th day to be about the same as those for the immediately preceding growth stages, but the correlations for growth increments may be expected to be of little value.

The problems which may be considered will be presented and discussed seriatim.

II. Analysis of Data.

Problem 1. The correlation between the absolute size of the organisms at its several periods of development.

When examined at an early stage of development, organisms are found to differ among themselves in size. The same is found to be the case when the same series is measured at a later growth stage or at maturity.

In the biological analysis of the phenomenon of growth a prob-

lem of great importance is that of the causes which bring about the differences in size observable at any stage of development, or after growth has entirely ceased. Are individuals which are found to be small at maturity those which were small initially and have remained so from the beginning, or may the growth rate of an individual change during the course of its development to such an extent that it may vary its position in the series under investigation from time to time? That the latter is to some extent the case we know from general observations on human children. The problem to be solved is that of the quantitative magnitude of the relationship between the size of the individual at different stages of development.

The nature of the biological problems to be investigated has been stated in earlier work, and an attempt has been made to solve them by grouping plants according to quintile (Pearl and Surface, 1915) or quartile (Reed, 1919) position in the culture to which they belong and ascertaining the quartile or quintile in which they fall at different stages of growth.

This method has the disadvantage that all the individuals, whatever their size, are lumped together in four or five groups. In this method of treatment, small differences between two individuals are, therefore, given as much significance as large ones, providing they are large enough to throw the two individuals into different quartiles or quintiles.

An alternative method, which will completely obviate this difficulty, is to determine the correlation between the sizes of the individual at different periods of growth. The possible correlations between the absolute size of the individuals in the II different stages of growth of the *Helianthus* plants are shown in Table III.

The coefficients in this table can be best understood by first examining those for the relationships between the sizes of the plants near the period of maturity, and then passing to the relationships between the sizes of the plants at earlier stages.

Considering first of all the coefficients in the lower right-hand corner of the table, we note that all the coefficients are very high, denoting practically perfect correlation. This is the relationship which would be expected for a period when the organism has

TABLE III.

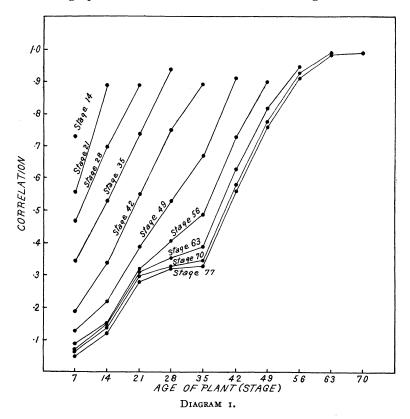
CORRELATION BETWEEN THE ACTUAL HEIGHT OF THE PLANTS AT THE VARIOUS GROWTH STAGES.

						Stage.					
Stage.	7	14	21	82	35	42	49	56	63	70	77
7		+.733 ±.041	+.733 ±.041 +.558 ±.061	+.468 ±.069	+.347 ±.078	+.193 ±.085	+.130±.087	+.093 ±.088	+.069±.088	+.00	+.053 ±.088
		6.71	9.14	6.78	4.46	2.26	1.50	1.05	0.78	0.74	09.0
41	$ +.733\pm.041$		4.889±.019	+.695 ±.046	$+.532\pm.064$	$ +.343\pm.078 $	+.220 ±.084	$+.151\pm.087$	+·150±.087	+.140 ±.087	十.123 ±.087
	17.9	9.71	48.0	15.2	8.38		2.00	1.74	1.73		1.41
21	+.558±.001	4.889±.019		+.887±.019	+.739 ±.040	+	$+.390\pm.075$	+.32	+.311±.080	+:2	+.282±.082
	9.14	48.0		47.1	18.4	8.97	5.20	4.02	3.90		3.40
28	$ +.468\pm.069 $	28 +.468 ±.069 +.695 ±.046 +.887 ±.019	$+.887 \pm .019$		$+.936\pm.011$	$ +.752\pm.038 $	$+.534\pm.063$	$+.409\pm.074$	$+.356\pm.077$	$+.329\pm.079$	$+.318\pm.080$
	6.78	15.2	47.1		85.2	9.61	8.44	5.55	4.61	4.17	3.99
35	十.347 土.078	$+.532\pm.064$	35 +.347 ±.078 +.532 ±.064 +.739 ±.040	+.936 ±.011		$+.892\pm.018$	$+.674\pm.048$	$+.488\pm.067$	$+.394\pm.075$	$+.350\pm.078$	$+.333\pm.079$
	4.46	8.38	18.4	85.2		49.5	13.9	7.24	5.26	4.50	4.23
42	$+.193\pm.085$	$+.343\pm.078$	$+.552\pm.062$	$+.752\pm.038$	$+.892\pm.018$		$+.914\pm.015$	$+.732\pm.041$	$+.629\pm.053$	$ +.580\pm.059 $	+.558 ±.061
	2.26	4.39	8.97	9.61	49.5		62.5	17.8	8.11	98.6	91.6
49	+.130±.087	$+.220\pm.084$	+.130±.087 +.220±.084 +.390±.075	$+.534\pm.063$	$+.674\pm.048$	$+.914\pm.015$		十.900 ±.017	$+.819\pm.029$	$+.775\pm.035$	$+.758\pm.038$
	1.50	2.60	5.20	8.44	13.9	62.5		53.5	28.1	21.9	20.1
20	+.093 ±.088	十.093 土.088 十.151 土.087 十.3	$+.320\pm.080$	+.409 ±.074	$+.488 \pm .067$	十.488 ±.067 十.732 ±.041	4.900 ±.017		+.948 ±.009	$+.926\pm.013$	4.911 ±.015
	1.05	1.74	4.02	5.55	7.24	17.8	53.5		105	73.3	60.2
63	4.069 ±.088	+.150±.087	$ +.069\pm.088 +.150\pm.087 +.311\pm.080$	+.356 ±.077	$+.394\pm.075$	$+.629\pm.053$	+.819±.029	十.948 土.009		$+.994\pm.001$	+.986 ±.002
	0.78	1.73	3.90	4.61	5.26	8.11	28.1	105		026	411
70	+.065 ±.088	+.140 ±.087	$+.297 \pm .081$	+.329 ±.079	$+.350\pm.078$	+	$+.775\pm.035$	+.926 ±.013	$+.994\pm.001$		$+.993\pm.001$
	0.74	1.62	3.67	4.17	4.50	9.80	21.9	73.3	046		828
11	$ +.053\pm.088 $	77 +.053 ±.088 +.123 ±.087 +.2	$+.282\pm.082$	282 ±.082 +.318 ±.080	$+.333\pm.079$	$+.558\pm.061$	+.758 ±.038 +.911 ±.015	+.911±.015	十.986 ±.002 十.993 ±.001	$+.993\pm.001$	
	09:0	1.41	3.46	3.99	4.23	91.6	20.1	60.2	411	828	

practically attained its adult size and in which there is relatively little change from one week to another.

As we follow the correlations between the later periods and preceding periods back, we note that there is a regular decrease in the values of the correlation coefficients. This may be best shown by summarizing the results graphically in diagram 1.

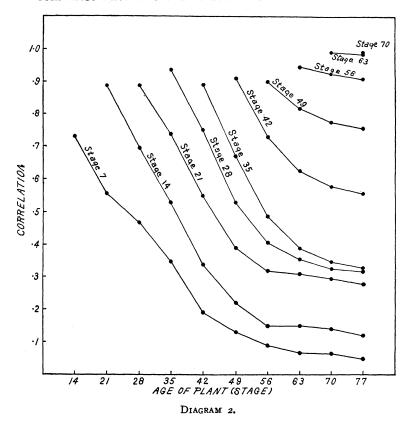
In the graph the correlation of the size of the organism at each



growth stage with its size at every antecedent growth stage (shown at the bottom of the diagram) is shown on the scale of correlation at the left by points marking the magnitude of the correlations for each of the growth stages. The pitch of the lines connecting the points for the 14th to the 77th growth stage shows the rapid decrease in the magnitude of the correlations as the stages become more widely separated in time.

The same type of diagram may be used to show the relationship between the size at early and at later growth stages. Diagram 2 shows the distribution of the magnitudes of the correlations for sizes of the individuals at the 7th to the 70th day (stage) and the size at subsequent growth stages.

From these lines it is clear that the correlations between size



at antecedent and subsequent periods decrease as the periods become more widely separated in time. This is true without exception for every period which furnishes evidence upon the question.

The coefficients are, however, positive in sign throughout, thus suggesting (though in some cases not proving) that throughout its growth period the size of the plant bears some relation to its size when first measured. This result is in agreement with the

findings of Webber (1920) in regard to the growth of Citrus stock.

Problem 2. The correlation between the growth increments of the organism during the several growth periods.

Our second problem is to determine whether there is a correlation in growth increments as well as in actual size of the organism. We shall thus answer the question whether the organism which grows more rapidly than the average during one growth period will grow more rapidly than the average in other growth periods and whether the organism which lags behind the average in its rate of growth during one growth period will also lag behind during other growth periods.

Little has heretofore been done towards the statistical treatment of growth increments. This is probably in part due to the arithmetical difficulties of computing the constants for increments, but if the moments and product moments be taken about zero as origin in computing the coefficients required under Problem I above, the calculations for growth increments are easily made by the use of formulæ given elsewhere (Harris, 1920).

The symmetrical table showing the relationship between the actual growth increments for all of the combinations of growth periods appears as Table IV. This table shows positive and statistically significant correlation coefficients for closely associated periods throughout the season up to and including the period for the 63d to the 70th day. The coefficients for the period from the 70th to the 77th day cannot in general be considered statistically significant in comparison with their probable errors.

Examining these results in a little greater detail, we note that the nine coefficients showing the relationship between the growth increments of successive weeks (the constants bordering the diagonal cell of the symmetrical table of constants) are all positive in sign and with the exception of the last (showing the relationship between the growth of the period from the 63d to 70th and that between the 70th to 77th day) all are statistically significant. The eight coefficients measuring the correlations between the growth increments of weekly periods which are separated by one week are also without exception positive, but are lower in magnitude and less certainly statistically significant. For periods more

TABLE IV.

CORRELATIONS BETWEEN THE GROWTH INCREMENTS DURING THE SEVERAL GROWTH PERIODS.

Growth				ANTICOL CONTINUENCY AND ANTICOL ANTICOL AND ANTICOL AND ANTICOL AND ANTICOL AND ANTICOL ANTICOL ANTICO	Growth	Growth Period.	The control of the co			
Period.	7 to 14.	14 to 21.	21 to 28.	28 to 35.	35 to 42.	42 to 49.	49 to 56.	56 to 63.	63 to 70.	70 to 77.
7 to 14		+.655 ±.051	+.259 ±.083	+.013 ±.089	115±.087	102 ±.088	095 ±.088	+.082 ±.088	070±.088	136±.087
14 to 21	14 to 21 +.655±.051	12.9	3.14 +.630±.053	0.14 +.264±.082	1.32 +.064±.088	1.17 024±.089	1.08 +.011 ±.089	0.93 +.100 ±.088	0.79 082±.088	1.57 047±.088
21 to 28	21 to 28 +.259±.083 +.630±.053	+.630±.053	11.8	3.21 +.636±.053	0.73 +.161 ±.086	0.27 079±.088	0.13 179±.086	1.14 140±.087	0.93 249±.083	0.53 023 ±.089
28 to 35	3.14 +.013 ±.089	28 to 35 +.013 ±.089 +.264 ±.082	+.63	12.1	1.80 +.532 ±.064	+.17	2.08 316±.080	$273\pm.082$	2.99 483 ±.068	0.20 169±.086
35 to 42	0.14 115±.087	35 to 42115±.087 +.064±.088	+.10	+.532 ±.064	8.37	1.70 +.778±.035	3.96 +.070±.088	3.33 +.067±.088	7.12 189±.085	1.97 106±.088
42 to 49	42 to 49102 ±.088	1.00	07	8.37 +.147 ±.087	+.7.	22.3	0.79 +.416±.073	0.70 +.250±.083	2.21 005±.089	1.21 +.038±.088
49 to 56	49 to 56095 ±.088	+.0	0.90 179±.086	1.70 316±.080	+.07	+.4	20.5	3.01 +.299±.081	+.453 ±.070	0.43 +.022 ±.089
56 to 63	56 to 63 +.082±.088	4.100±.088	140±.087	3.90 273±.082	+.067±.088	5.07 +.250±.083	+.299 ±.081	o. v	+.476±.069 +.188±.085	+.188±.085
63 to 70	63 to 70070±.088	90.	249±.083	3:33 483±.068	189±.085	3.01 005±.089	3.73 +.453 ±.070	+.476±.069	10.0	4.086±.088
70 to 77	780	0.93 047 ±.088 0.53	023±.089 0.26	169±.086 1.97	105±.088	+.038 ±.088	0.44 +.022 ±.089 0.25	+.022 ±.089 +.188 ±.085 +.086 ±.088 0.25 2.20 0.97	+.086±.088 0.97	76.0

widely separated in time the correlations are in part positive and in part negative in sign.

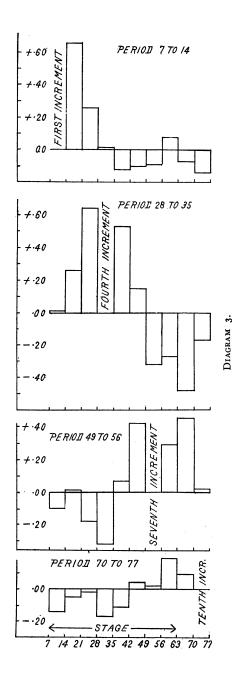
Thus from the results as a whole it appears that the increments of successive periods are generally positive and fairly highly correlated when the periods show actual growth increments. Thus the zone of coefficients lying along the diagonal cell are positive and generally fairly high. When the periods are separated by any considerable length of time the coefficients are generally insignificant in magnitude and may, as a matter of fact, be either positive or negative in sign.

The relationship may be brought out by determining the averages of the correlation coefficients, with regard to sign, for the increments of periods separated by various lengths of time. The results are as follows.

0 9 +.5009 1 8 +.2240 2 7 0334 3 6 1236 4 5 1640 5 4 1033
2 7 —.0334 3 6 —.1236 4 5 —.1640
3 6 —.1236 4 5 —.1640
4 5 —.1640
,
5 4 —.1033
6 3 —.0077
7 2 —.0585
8 ı —.1360

If we disregard the cases in which there are less than five coefficients to be averaged, we note a steady decrease in the magnitude of the correlation coefficient. Periods of growth which are successive or separated by only one week have positively correlated growth increments. Periods which are more widely separated show negative correlations of the increments.

The relationship between the coefficients in Table IV. may be clarified by diagram 3 which shows the relationship between four of the ten growth increments and each of the other ten increments. The increments selected as a "first variable" in the correlation are the first, fourth, seventh, and tenth. This has the advantage of representing the first and the last growth increment, and of leaving undrawn no more than two successive increments. The figures are aligned according to the ten increments representing the "second variable" of the correlation.



The graphs for the first, fourth and seventh increment show clearly the shift in the position of the maximum positive correlation from the earlier to the later periods as the "first variable" is chosen from the later periods. The same is shown less clearly by the correlations for the tenth increment, but there the coefficients are very small, presumably because growth has practically ceased.

It is clear, therefore, that plants which are growing more rapidly during any period of development will grow more rapidly during a closely associated subsequent period of development but that there is little or no relationship, or even a negative relationship, between the rate of growth of the organisms studied at considerably separated periods of time.

Since the correlations for absolute growth increments are so small for all except successive periods of time, it seems unnecessary to deal at present with the relative growth increments, *i.e.*, with the growth increments expressed as a fraction of the size of the organisms at the beginning of the growth period.

Problem 3. The correlation between the absolute size of the organism at given stages of development and subsequent growth increments.

In the higher plant organism rate of growth at any period must be supposed to depend to some extent upon plastic materials synthesized by the more nearly mature portions of the same individual. Thus one might expect to find a relationship between the actual size of the organism at any stage of growth and the rate at which the organism increases in size during a subsequent period.

We have determined the possible correlations between the absolute size of the organism at different periods and the growth increment of the organism during subsequent growth periods. The coefficients are presented in Table V. This shows positive correlation between the actual size of the organism at every stage of development from the 7th to the 70th day and the increase in the size of the organism during the following week. The magnitude of the correlation is of the order r=0.45 to r=0.60 for the 7th, 14th, 21st, and 28th day. For these growth stages the correlation between actual size and the subsequent growth incre-

FABLE V.

CORRELATIONS BETWEEN HEIGHT AT EACH GROWTH STAGE AND THE INCREMENTS AT SUBSEQUENT GROWTH PERIODS.

B.e-			AND THE PROPERTY OF THE PROPER	THE PROPERTY OF THE PROPERTY O	Growth	Growth Period.		Spring to the same of the same	Annual Laurent Carles of Principles and Principles	
Sia	7 to 14.	14 to 21.	21 to 28.	28 to 35.	35 to 42.	42 to 49.	49 to 56.	56 to 63.	63 to 70.	70 to 77.
7	+.503 ±.066 +.28	+.285±.081	35 ±.081 +.239 ±.084028 ±.089162 ±.086	028 ±.089	162 ±.086	036±.088	046±.088	042 ±.088	021±.088	100年.088
	09.2	3.50	2.86	0.32	1.88	0.41		0.47	0.24	1.14
14		+.611±.056	+.611±.056 +.285±.081 +.000±.089 146±.087	4.000 ±.089	146±.087	093 ±.088	090 ±.088	+.050±.088	062 ±.088	71
		0.11	3.50	10.0	1.68	90.1		0.57	0.70	1.63
21			+.517±.065	十.517 土.065 十.153 土.087	$041 \pm .088$	F063 ±.088	042±.088	+.084±.088	081±.088	1 03 ±.088
			2.96	1.77	0.46	0.72	0.48	96.0	0.92	1.18
28				+.436 ±.072 +.062 ±.088	$+.062\pm.088$	880	$122\pm.087$		024±.089183±.086	075 ±.088
				80.9	0.70	0.92	1.40	0.27	2.14	0.85
35					$+.255\pm.083$	004 ±.089	1.2		一.125 ±.087 329 ±.079	124 ±.087
					3.09	0.05	2.57	1.43	4.17	1.42
42						+.360±.077	135±.087		$065 \pm .088343 \pm .078$	$145\pm.087$
						4.67	1.56	0.74	4.39	1.67
49		-					十.079 土.088		十.059 ±.088 (一.262 ±.083	$093\pm.088$
							0.89	29.0	3.17	1.06
26								+.182 ±.086	$029\pm.089$	071±.088
-								2.12	0.32	0.81
63									十.129 ±.087	$002 \pm .089$
									1.48	0.03
20										4.007 ±.089
_										0.08

ment is clearly significant in comparison with its probable error. The coefficients are lower for the 35th and the 42d day, but are probably statistically trustworthy. Beyond this period there seems to be no relationship between the size of the organism and its growth rate in an immediately following period.

For the first two stages of growth measured, the 7th and the 14th day, there may be a significant correlation of the order r = +.285 between size and growth increments during the second following week.

The coefficient of correlation between size and the increment in the second week following is also positive for the 21st and 28th day, but neither of these values may be considered statistically significant in comparison with its probable error. Finally for the first stage (seventh day) there may be a significant correlation between absolute size and growth increments during the third week following (r=+.239 for increment for 21st to 28th day). Other than this the coefficients are for the most part statistically insignificant in comparison with their probable error.

Summarizing the preceding statements as a basis for further analysis, we note that for the first six growth stages (7th to 42d day) there is a significant positive correlation between the size of the organism at the given stage and the growth increment of the following week. For the first two growth stages (and possibly in the third where $r/E_r = 1.77$) there is a significant correlation between the size of the organism and the growth increment in the second subsequent week. Finally, for the first stage only, there is a significant positive correlation between size and growth increment in the third subsequent week.

Disregarding these 9 coefficients and the 4 positive but not significant correlations between the sizes at the several growth stages and the growth increments of the following week, we may note the following facts concerning the remaining 42 coefficients.

Of these 42 coefficients 36 are negative while only 6 are positive in sign. Of the 6 positive coefficients only that between actual size on the 21st day and growth increment between the 28th and 35th day (already considered above) is as large as its probable error. Of the 36 negative coefficients 18 are larger than

their probable error, and 5 of these are over twice as large as their probable error.

There is, therefore, clear evidence that the subsequent growth of the higher plant organism is measurably conditioned by its size. In general the larger individuals grow more rapidly in immediately subsequent periods, but somewhat more slowly than the average in more distant subsequent periods.

While a detailed discussion of the relation of these results to the theory that growth may be satisfactorily described by the curve of an autocatylic reaction falls quite outside the scope of this paper, it must be noted that negative correlations between actual size at a given stage and the growth increments of certain subsequent growth periods might be expected. As Reed and Holland (1919) have pointed out the plants attained about half their final height at about the thirty-fourth day. From this time on the increments were decreasing. Plants which had attained more than the average size at this period would, therefore, of necessity, make smaller average increase in size in later periods.

The number of individuals measured is not sufficiently large to carry the analysis farther.

III. RECAPITULATION.

The purpose of this paper has been to illustrate on the basis of a specific series of data the value of the inter-periodic correlation coefficient in the analysis of the phenomena of growth.

The analysis shows that in the case of a series of *Helianthus* plants the actual size of the individual at any stage of development is closely correlated with its size at other closely associated stages of development. The magnitude of the correlation rapidly diminishes as the growth stages become more widely separated in time. Thus the final size of the organism is but to a slight extent determined by its initial size.

The correlation between successive growth increments is positive in sign and statistically significant, with the general average of \bar{r} =.501. The correlation for increments of weekly periods separated by one week is on the average only about \bar{r} =.225. For periods more widely separated than this the correlation between growth increments is on the average negative in sign.

Thus plants which are growing more rapidly during one period of development will grow more rapidly during a closely associated period, but there is little or no relationship between the growth increments of more widely separated periods.

The growth increment of the organism is positively correlated with its size at an immediately preceding stage. In the early stages of growth, the growth increments of two or even three subsequent periods are positively correlated with the initial size of the organism.

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